

CURRENT LITERATURE

NOTES FOR STUDENTS

Hybrid vigor.—The phenomenon of hybrid vigor has come to hold a very important place in practical plant breeding, and is of considerable theoretical interest to geneticists. The most generally accepted interpretation has been EAST'S¹ "heterozygosis," according to which hybrids are vigorous because of their heterozygous sets. Heterozygosis has been very valuable in helping to organize our ideas on the general subject of hybrid vigor, but as a theoretical explanation of the phenomenon involved it has been unsatisfactory. When one says that hybrids are vigorous because of their heterozygous sets, he is making an accurate restatement of the fact of hybrid vigor in the language of genetics, but he is not providing any real explanation of the phenomenon.

The only acceptable "real" explanation that has yet been presented is as follows. In nature a "struggle for existence" occurs among species and individuals. There occurs also a struggle for existence among unit characters. If a unit character is undesirable it is eliminated, since the species possessing it is eliminated. The unit characters, therefore, that have survived and appear in the plants of today are for the most part "desirable" ones, although some undesirable ones also may have survived, having been carried through in association with the "desirable" characters. The majority of unit characters today, however, may certainly be regarded as "desirable" ones, and a majority is sufficient for the present argument.

The question then is raised as to what constitutes a so-called "desirable" character. It may, of course, be any one of a number of things, but is there not some feature common to all such "desirable" characters? The character would seem to be vigor. Each "desirable" character must add somewhat to the vigor of the plant that contains it, and if vigor is increased, such things as size and productiveness will also be increased. Those plants, therefore, will be most vigorous which have in combination the greatest number of "desirable" characters.

The next question is, what plants, in general, have in combination the greatest number of desirable characters? The answer is hybrids, for they combine the "desirable" characters of both parents. Thus, in general, hybrids have twice as many "desirable" characters as do pure races. At this point the objection is raised that though hybrids do actually contain this double quota,

¹ EAST, E. M., and HAYES, H. K., Heterozygosis in evolution and in plant breeding. U.S. Dept. Agric., Bur. Pl. Ind. Bull. no. 243. pp. 58. 1912.

each character is represented by only a single dose in the hybrid and by a double dose in the pure race, so that mathematically the two situations are equivalent. This objection is valid only if we assume complete lack of dominance. We are certainly within our rights in assuming some slight degree of dominance, and if we do this it follows that hybrids have more in the way of active "desirable" characters than have pure races, and, having more "desirable" characters, hybrids are more vigorous. They are vigorous, not because they contain more heterozygous sets, but because they contain more positive dominant characters.

This is a rather obvious explanation of hybrid vigor, and one that has probably occurred to a number of geneticists, being commonly referred to as "the hypothesis of dominance" (accounting for hybrid vigor). It involves 3 assumptions: (1) that there is such a thing as dominance; (2) that most dominant characters are "desirable" ones, that is, of survival value; this assumption is rendered easier if we accept the presence and absence hypothesis; (3) that these dominant "desirable" characters add more vigor than they detract from it, and add to vigor *to the degree in which they are dominant*. This last assumption is the critical one; but even that seems very reasonable.

KEEBLE and PELLEW² suggested this explanation in 1910, and since then it has had some discussion in the literature. At first statement the theory seems sound, but actually it does not fit the facts. The two chief objections to this theory of dominance may be found in the publications of SHULL, EMERSON, and EAST (*loc. cit.*).

1. If hybrid vigor were due to dominance, it would be possible in generations subsequent to the F_2 to recombine in one race all of the dominant determiners. Thus there could be isolated a race that was "100 per cent vigorous," and since it would be homozygous, its vigor would not be lost by inbreeding. Actually, though, hybrid vigor cannot be fixed in this way; "all maize varieties lose vigor when inbred."

2. Experience assures us that the distribution of individuals in the F_2 generation with reference to hybrid vigor is represented graphically by a symmetrical curve similar to the normal probabilities curve; the class containing the greatest number of individuals is that which shows the medium amount of hybrid vigor, while on either side of this class the fall in the curve is regular, reaching its lowest point in the two small extreme classes which show respectively greatest hybrid vigor and least hybrid vigor. According to the dominance hypothesis, however, the largest class of F_2 individuals would be that showing the greatest hybrid vigor, while the smallest class would be that showing least hybrid vigor. The curve representing such a situation would be unsymmetrical and strikingly different from that which actually occurs. For these two reasons the dominance hypothesis seems to have been discarded.

² KEEBLE, F., and PELLEW, C., The mode of inheritance of stature and time of flowering of peas (*Pisum sativum*). Jour. Genetics 1:47-56. 1910.

Although it is theoretically attractive, its failure to satisfy these two important details of the hybrid vigor situation has condemned it.

JONES³ has ingeniously modified the dominance hypothesis so as to avoid these difficulties. At first consideration his theory seems to be clearly the most reasonable explanation of hybrid vigor that has yet been presented, although in time it may encounter destructive criticism. The argument is essentially the same as that for the old dominance hypothesis, with the following important modification. Assume that one parent contains the dominant determiner *A*, linked with the recessive *c*; on another chromosome it contains *B* linked with *d*. The total formula may be expressed conveniently as *Ac, Bd*. The other parent has the formula *aC, bD*. The hybrid is more vigorous than either parent because it combines all 4 dominant determiners. The attractiveness of this scheme is that it escapes the objections that were made to the older dominance hypothesis: (1) the fact that 100 per cent hybrid vigor cannot be fixed is quite in accordance with JONES' scheme, for it is obviously impossible to isolate a homozygous race, combining the 4 dominant determiners, *A*, *B*, *C*, and *D* (unless crossing over occurs); (2) a simple mathematical demonstration will show that the distribution of F_2 individuals (with respect to hybrid vigor) is quite what it should be, represented by a symmetrical curve, similar to the curve of probabilities. In fact, this new theory, "the dominance of linked factors," seems altogether sound. We should reasonably expect that each chromosome would contain one or more dominant determiners (conducive to vigor) linked with one or more recessives. In this day of factors and determiners such a hypothesis is quite appropriate. It may be, however, that in the future such a phenomenon as hybrid vigor may be explained on the basis of the stabilities and reactivities of the constituents of specific protoplasts.—
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Taxonomic notes.—BLAKE⁴ has published a fascicle of papers containing descriptions of new species. In the paper dealing with Compositae new species are described in *Aphanostephus*, *Diplostephium*, *Verbesina*, *Liabum*, and *Cirsium*. Collections from Venezuela and Curaçao contain new species in the following genera: *Ruprechtia* (2), *Atriplex*, *Bauhinia*, *Croton* (2), *Maytenus*, *Zizyphus*, *Vismia*, *Hecatostemon* (a new genus of Flacourtiaceae), *Passiflora*, *Jacquinia*, *Bumelia*, *Aspidosperma*, *Plumeria*, *Marsdenia* (2), *Lycium*, *Tabebuia*, *Dianthera*, *Oxycarpha* (a new genus of Compositae), *Simsia*, and *Verbesina*. The new species from Oaxaca are referred to *Iresine* (2), *Amyris*, *Guarea*, *Tri-*

³ JONES, D. F., Dominance of linked factors and heterosis. *Genetics* 2:466-479. 1917.

⁴ BLAKE, S. F., II. Further new or noteworthy Compositae. *Contrib. Gray Herb. N.S.* no. 53. pp. 23-30. 1918.

———, New Spermatophytes collected in Venezuela and Curaçao by Messrs. Curran and Haman. *Ibid.* pp. 30-55.

———, New plants from Oaxaca. *Ibid.* pp. 55-65.